TRANSMISSION AND SIGNIFICANCE OF B CHROMOSOMES IN *ANTHURIUM WAROCQUEANUM* J. MOORE

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

IN HORTICULTURE

AUGUST 1980

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ABSTRACT

Somatic and meiotic chromosomes of Anthurium warocqueanum J. Moore and its selfed offspring were analyzed. The parent showed 2n=30 + 3B in both somatic cells and pollen mother cells. In somatic cell division B chromosomes behaved regularly, whereas their meiotic activities were found to be variable. Three configurations of 3 B chromosomes were observed at metaphase I of parent meiosis: one trivalent, one bivalent and one univalent, and three univalents. At anaphase I univalent B chromosomes tended to lag and eventually form micronuclei.

The number of B chromosomes in offspring ranged from 0 to 6, indicating their transmission from both male and female gametes. The offspring with 2 B chromosomes appeared in greatest frequency. It was hypothesized that both male and female gametes frequently contained one B chromosome through the normal distribution of the bivalent B at meiosis and the elimination of the univalent B due to lagging.

Investigation on pollen mother cells of offspring also revealed irregular behavior of B chromosomes. When two or more B chromosomes were present, 2 Bs were often associated together at early meiotic stages and had normal disjunction at anaphase I. In contrast, univalent B chromosomes showed variable movements during anaphase I; moving toward either poles, lagging, or two sister chromatids separating to opposite poles. With the higher

number of B chromosomes, normal A chromosome bivalent formation seemed to be reduced.

No distinct phenotypic effects of B chromosomes in Anthurium warocqueanum were observed.

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I. INTRODUCTION

Anthurium warocqueanum J. Moore, a native of Colombia, belongs to the largest genus in Araceae. This species, cultivated for its velvety foliage, is taxonomically placed in Sect. Cardiolonchium Schott (Engler, 1905) in which B chromosomes are very common (Sheffer and Kamemoto, 1976a).

The chromosome number of A. warocqueanum has been determined to be 2n= ca. 30 by Gaiser (1927), n=15 by Pfitzer (1957) and 2n=30+3B by Sheffer and Kamemoto (1976a). Kaneko and Kamemoto (1979) analyzed the karyotype of A. warocqueanum with 2n=30+3B and reported that the three B chromosomes were submetacentrics of about half the size of the smallest A chromosomes or autosomal chromosomes.

The inheritance of B chromosomes is non-Mendelian (Jones, 1975). In many plants and animals the distribution of B chromosomes through meiosis has been found to be very irregular (Jones, 1975; Müntzing, 1974; Battaglia, 1964). Nine offspring of A. warocqueanum (2n=30+3B) selfed fell into three classes of somatic chromosomes: 2n=30+2B, 2n=30+3B and 2n=30+4B (Kaneko and Kamemoto, 1979).

In the present study A. warocqueanum with 2n=30+3B and its 104 selfed offspring were investigated to elucidate the transmission and inheritance of B chromosomes, to determine the effect of B chromosomes on meiotic behavior, and to examine the effects of B chromosomes on plant morphology and plant development.

II. REVIEW OF LITERATURE

B chromosomes, which are also commonly called supernumerary or accessory chromosomes, are additional chromosomes to the main chromosome complement in an organism. They are found in both animals and plants and exhibit great variation in terms of the number and structure within a species, or in some cases within an individual organism. In general, B chromosomes are smaller than normal (A) chromosomes, possess no distinct phenotypic effect, and often show irregular transmission during meiosis and/or mitosis. No homologous pairings between B chromosomes and A chromosomes at meiosis have been seen, and yet it is assumed that B chromosomes are derived from A chromosomes (Jones, 1975).

Occurrence of B chromosomes in plants

Although B chromosomes are found in both plants and animals, their occurrence is more frequent in plants. Findings of variable chromosome numbers (Kuwada, 1915; Reeves, 1925) and the recognition of the presence of small extra bodies in meiosis (Fisk, 1925) led to the first studies of B chromosomes in plants done in maize (Longley, 1927). Longley (1927) examined the behavior of an extra chromosome in the microspore mother cell and studied the size and shape of the chromosome. Information on the distribution of the B chromosomes among plants has been

given by Darlington and Wylie (1955), Battaglia (1964), Federov (1969), Jones (1975, 1976), and Rees and Jones (1977). In the most recent survey, Rees and Jones (1977) reported that 644 species of flowering plants contained B chromosomes. Seven species belong to the class gymnosperm. Among 637 B chromosome-containing angiosperm species, 318 were dicotyledons and 319 monocotyledons (Rees and Jones, 1977). Having insufficient cytological information on a large number of plant species, Darlington (1956) estimated that B chromosomes occur in as many as 10 % of flowering plants, and also pointed out that in many cases chromosome counts were based on examination of a single individual of a species.

According to Jones (1975), B chromosomes are much more common in certain angiosperm families such as the Compositae in the dicotyledons, and Gramineae, Liliaceae, and Amaryllidaceae in the monocotyledons. Admitting the lack of cytological observations on many plant species, he suggested the possibility of more frequent B chromosome occurrence in highly evolved herbaceous families of angiosperms. In 1968, B chromosomes were reported for the first time for six woody angiosperms in the Himalayas (Mehra and Bawa, 1968) and later in the tree Ficus krishnae (Joshi and Raghuvanshi, 1970).

Inbreeding species have rarely shown the appearance of B chromosomes. The positive correlation between outbreeding and the presence of B chromosomes was

demonstrated by Moss (1969) in experiments with rye where B chromosomes caused a greater reduction in fertility when the plant was selfed than when crossed.

Proportionally, B chromosomes were found as frequently in polyploid plants as in diploids (Jones, 1975; Rees and Jones, 1977). However, there was the interesting case of Ranunculus ficaria from Britain where B chromosomes occurred only in diploid plants but not in tetraploids (Gill et al., 1972).

In natural populations, the geographic distribution of B chromosomes within a single species may vary. Several studies have attempted to show the adaptive advantage of B-chromosome plants in natural habitats. Fröst (1958a), for example, studied 222 populations of Centaurea scabiosa in northern Europe and showed that populations with a higher number of B chromosomes were frequently found at lower, humid areas. Bosemark (1956) found differences in the occurrence of B chromosomes in Festuca pratensis in different areas in Sweden and suggested a positive correlation between clay content of the soil and the frequency of B chromosomes. Similar population studies have been done in Clarkia williamsonii (Wedberg et al., 1968), Allium cernum (Grun, 1959), Clarkia elegans (Mooring, 1960), Caltha palustris (Kootin-Sanwu and Woodell, 1969), Crepis conyzaefolia (Fröst, 1962), Dactylis glomerata (Zohary and Ashkenazi, 1958), Phleum phleoides (Bosemark, 1967), Ranunculus ficaria

(Gill et al., 1972), Secale cereale (Müntzing, 1950, 1957), Tainia laxiflora (Tanaka and Matsuda, 1972), Zea mays (Longley, 1938), and Alopecurus pratensis (Rapp, 1979).

The highest number of B chromosomes in a natural population, 16, was found in Centaurea scabiosa (Fröst, 1958b). Experimentally, 34 B chromosomes were obtained in maize (Randolph, 1941).

Major characteristics of B chromosomes

1. Structure of B chromosomes

B chromosomes are characteristically smaller than A chromosomes. They are first recognized in species by their small size at meiosis and mitosis. For example, the typical B chromosome of corn was found to be about half the length of the shortest A chromosome (Carlson, 1978) and appeared to have a subterminal constriction (Randolph, 1941).

A second characteristic of B chromosomes is their heterochromatic nature. B chromosomes tend to be darkly stained at interphase and early prophase, especially in animal cells. In plants, Jones (1975) listed an equal number of plants with heterochromatic B chromosomes and those with euchromatic ones.

Active genes are absent in B chromosomes. The search for possible gene loci in B chromosomes of maize was unsuccessful (Randolph, 1941). The biochemical studies of B chromosome DNA in maize (Chilton and McCarthy, 1973) and

in rye (Rimpan and Flavell, 1976) showed that A and B chromosome DNAs were very similar in their composition. Yet, the detailed genetic organization of B chromosome is still undetermined. Although nucleolar organizers are generally lacking in B chromosomes, Rimpan and Flavell (1976) found the presence of ribosomal RNA genes on B chromosomes from a certain rye.

2. The behavior of B chromosomes at somatic cell division

In many plant species B chromosomes are generally transmitted very regularly at somatic cell divisions. Jones (1975) listed mitotically stable and unstable plants and surveyed patterns of instability in B chromosome systems. An example of noticeable B chromosome instability was reported in Crepis capillaris (Rutishauser and Röthlisberger, 1966) in which, although the rosette plants had constant B chromosome numbers, stems, bracts, young inflorescences, receptacles, and florets varied in their number. Röthlisberger (1970) suggested that the instability of B chromosomes was coincident with flower initiation.

3. Meiotic behavior of B chromosomes

At metaphase I, B chromosomes do not pair with A chromosomes, but tend to appear as univalents. When more than one B chromosome is present, they are capable of forming bivalents, the most frequent configuration, and in some cases multivalents such as trivalents and quadrivalents in addition to univalents (Jones, 1975). Very interesting interarm pairing of univalent B chromosomes was reported in

Poa trivialis and Holcus lanatus (Bosemark, 1957).

The movements of B chromosomes at anaphase I and anaphase II varies. In some species such as Festuca pratensis (Bosemark, 1954), F. arundinacea (Bosemark, 1957), and Poa trivialis (Bosemark, 1957), B chromosomes divide at anaphase I, whereas they separate at anaphase II in some other species like Plantago serraria (Fröst, 1959) and Ranunculus acris (Fröst, 1969). The accumulation mechanism of B chromosomes has been explained by their unusual behavior at AI and AII (Battaglia, 1964; Müntzing, 1974; Jones, 1975).

Nondisjunction occurring at a post-meiotic division may also contribute to the accumulation of B chromosomes. Directed nondisjunction in pollen mitosis was reported for the first time in rye by Hasegawa (1934). Håkansson (1948) found a similar situation in the first mitosis of the egg cell in the same plant. In Hypochoeris maculata, however, the inheritance of B chromosomes was reported to be different between male and female meiosis such that Bs accumulated on the female side while random transmission of Bs occurred on the male side (Parker, 1976).

Effects of B chromosomes

1. Effect on general plant development

Normally the phenotypes of plants are not distinguishably affected by the presence of B chromosomes aside from two exceptions reported in Haplopappus gracilis and

Plantago coronopus. Jackson and Newmark (1960) reported a color change in the achenes from brownish-red to dark purple when Haplopappus gracilis contained a B chromosome, while in Plantago coronopus, Paliwal and Hyde (1959) found complete male sterility due to the presence of B chromosomes. The general B-chromosome effects in plants were reviewed by Battaglia (1964) and Jones (1975) and they concluded that low numbers of Bs had neutral effects whereas with high numbers plants might have reduced fertility and vigor. Müntzing (1963) demonstrated the influence of B chromosomes on vegetative characters in rye; the straw weight and tiller number were reduced with higher numbers of B chromosomes and odd-numbered Bs had a more severe effect on reduction of plant growth than did even-numbered Bs. In Lolium perenne, on the other hand, Teoh et al. (1976) showed a selective advantage of plants with B chromosomes under high sowing density conditions.

2. Effects on A chromosomes

The effect of B chromosomes on chiasma frequency and distribution of A chromosomes has been investigated by many researchers. Increased recombination in A chromosomes in the presence of Bs has been reported in some species such as Zea mays (Ayonoadu and Rees, 1968; Hanson, 1969; Chang and Kikudome, 1971; Ward, 1973), while a reduction of A chromosome chiasma frequency was observed in some other plants like Lolium perenne (Cameron and Rees, 1967). The B-chromosome control over A-chromosome pairings in

some hybrid plants is interesting. Evans and Macefield (1973) reported that in the diploid hybrid (Lolium perenne X L. temulentum), B chromosomes suppressed the homoeologous pairings between two genomes. In contrast, the tetraploid hybrid synthesized from the diploid hybrids showed multivalent formations when B chromosomes were absent, and with Bs there were only the homologous pairings that is typical in an allotetraploid.

Origin of B chromosomes

The origin of B chromosomes is uncertain. Some schemes for the origin of B chromosomes in plants have been proposed by several cytologists. Chromosome breakage at the weak secondary constriction and dissociation of the satellite from the main chromosome body had been suggested as one of the mechanisms of production of B chromosomes (Battaglia, 1964). In Tradescantia paludosa, Swanson (1943) hypothesized chromosomal fragmentation by a translocation event. B chromosomes in Lolium were assumed to be results of longitudinal misdivision of A chromosome univalents or misdivision of the centromere during prometaphase (Hovin and Hill, 1966). B-chromosome polymorphism due to centromere misdivision and deletion of standard fragment is very common in rye (Jones, 1977). Rapp (1979) studied Alopecurus pratensis and hypothesized the origin of B chromosomes starting with a paracentric inversion, crossing over within the inversion loop, and formation of anaphase

bridge. He also showed the transmission mechanism of B chromosome through further generations. It was suggested that the evolution of B chromosomes from A chromosomes in Solanum viarum was a long process and that increasing breakability and heterochromatization of fragments had led to the status of neutral and dispensable B chromosome (Dnyansagar and Pingle, 1979).

B chromosome studies in Anthurium

B chromosomes in the genus Anthurium were observed for the first time in A. crystallinum (n=15+ 0-2B), A. forgetti (n=15+ 0-2B), and A. magnificum (n=15+ 0-2B) by Pfitzer (1957). Sheffer and Kamemoto (1976a) determined chromosome numbers of 63 Anthurium species and found frequent occurrences of B chromosomes in the Sect. Cardiolonchium with numbers varying from one to three. Seven species were listed to have B chromosomes; A. trianae (2n=28, 29+1B), A. crystallinum (2n=30+1B), A. regale (2n=30+1B), A. splendidum (2n=30+2B), A. wallisii (2n=30+2B), A. walujewii (2n=30+2B), and A. warocqueanum (2n=30+3B) (Sheffer and Kamemoto, 1976a, 1976b).

Sharma and Bhattacharyya (1961) analyzed the karyotypes of A. glaziovii and three varieties of A. andraeanum, and discovered that different populations of the same species had different numbers of B chromosomes.

Tsuchiya and Takada (1962) reported the chromosome number of 2n=32 for A. andraeanum, an important cut flower.

However, Kaneko and Kamemoto (1978) suggested that the smallest pair might be accessory chromosomes, based on the presence of 2B chromosomes in a white cultivar 'Uniwai'.

The meiotic behavior and transmission of B chromosomes in Anthurium were reported in A. andraeanum 'Uniwai' (Kaneko and Kamemoto, 1978) and A. warocqueanum (Kaneko and Kamemoto, 1979). At metaphase I of meiosis in pollen mother cells, 2 B chromosomes in 'Uniwai' were either paired or remained unpaired (Kaneko and Kamemoto, 1978). The selfed A. warocqueanum (2n=30+3B) produced offspring with 2, 3 and 4 B chromosomes, indicating that B chromosomes were transmitted through both male and female gametes (Kaneko and Kamemoto, 1979).

III. MATERIALS AND METHODS

The clone of Anthurium warocqueanum (Fig. 1) was available in the collection of the University of Hawaii. The chromosome number of the clone was determined earlier by Sheffer and Kamemoto (1976a) and Kaneko and Kamemoto (1979) as 2n=30+3B.

Seeds of self-pollinated A. warocqueanum were germinated on finely chopped tree fern fiber on February 19, 1976. Seedlings were transplanted into flats filled with chopped tree fern fiber on December 28, 1976, individually into 6-inch pots, and finally into deeper 6-inch pots with wood shavings as the medium on August 4, 1978. The selfed progeny of 104 offspring was grown under 80 % saranshade.

Chromosome numbers were determined by examining both somatic cells from actively growing root tips and pollen mother cells from anthers. For the study of mitotic chromosomes, root tips were sampled between 8:00 a.m. and 10:00 a.m. and placed in a pretreatment solution of 0.002 M 8-hydroxyquinoline or 15-20 ppm o-isopropyl-N-phenyl-carbamate (IPC) for 3-5 hours at about 18 °C. After fixing in 2:1:1 Carnoy's solution (95 % ethyl alcohol, chloroform, and glacial acetic acid) for 20 minutes at 18 °C. and hydrolyzing in 1 N hydrochloric acid for 10 minutes at 50 °C., root tips were washed in tap water and placed in 45 % acetic acid for 10 minutes. On a microscope slide root caps were removed under a dissecting microscope and the remaining root tissues were squashed in 1 % aceto-orcein

after applying a cover slip. Air bubbles were removed by gentle tapping of the cover slip with the point of a dissecting needle. The slide was placed in a saturated 45 % acetic acid chamber for about 30 minutes. The excess stain was removed, the slide was heated gently, and the cover slip was pressed firmly. The edges of the cover slip were then sealed with dental wax. The preparation was examined under a light microscope.

For meiotic analysis, spadices were fixed in Carnoy's mixture of 6:3:1 (chloroform, 95 % ethyl alcohol, and glacial acetic acid) for at least 24 hours at room temperature (ca. 24°C.) and stored in a freezer at minus 10°C. Anthers dissected out from a spadix were squashed in 45 % acetic acid. After blotting out the excess acetic acid and removing the anther walls, a drop of 1 % aceto-orcein was added to the pollen mother cells. A cover slip was placed over the cells, and air bubbles were removed. The slide was heated for a few seconds and then pressed in bibulous paper to remove excess stain and to flatten the cells. Dental wax was applied to seal the edges of the cover slip. Meiotic behavior of chromosomes was studied under 40X and 100X oil objectives of a light microscope. Diakinesis and metaphase I were investigated to determine the chromosome number of a plant.

The pollen grains were stained with acetocarmine for 1-2 hours and examined under a light microscope to determine pollen stainability as a possible indication of

the pollen fertility of the plant.

Photomicrographs of selected mitotic and meiotic chromosomes were taken with a Zeiss photomicroscope at a magnification of 550X on Kodak High Contrast Copy film.

Karyotypes were made by cutting each chromosome from a print that was enlarged from a photomicrograph negative and arranging the chromosomes in descending order of length.

To determine the effects of B chromosomes in the offspring of selfed Anthurium warocqueanum, leaf length, leaf width, increase in stem length, and date of first flowering were investigated. Both length and width of the largest leaf of each plant were measured on August 4, 1978, February 6, 1979, and August 9, 1979. Increase in stem length was determined after the final transplanting to 6-inch pots. A piece of thin wire was stretched across the top of the pot to give a base line (reference line). The distance from this base line to the base of the petiole of the youngest leaf was measured; a positive measurement being above the base line and a negative measurement being below. Three measurements were done in 6-month intervals; August 15, 1978, February 6, 1979 and August 9, 1979. Absolute differences between measurements were calculated in order to determine the increase in the rate of growth of the stem length of each offsping. The date of first flowering was recorded when the young inflorescence emerged and became visible. Means of observations and standard

errors were calculated in each B-class. Effects of B chromosomes on plant phenotype were examined by carrying out a regression analysis.

Plate I

Figure:

1. Photo of the parent *Anthurium warocqueanum*


1

IV. RESULTS AND DISCUSSION

Cytology of the parent

The somatic chromosome number of Anthurium warocqueanum was determined to be 2n=30+3B (Fig. 2). This determination confirms the earlier report of Sheffer and Kamemoto (1976a). The karyotype (Fig. 3) consists of 2 pairs of large chromosomes, 12 pairs of medium to small chromosomes, 1 pair of satellite chromosomes, and 3 B chromosomes which are about half the size of the smallest A (autosomal) chromosomes. This result does not differ from the analysis of Kaneko and Kamemoto (1979).

Observation of PMCs in the parent (Figs. 4 - 16) showed the presence of three B chromosomes. At diakinesis and metaphase I there were three different configurations of the 3 Bs; 1 trivalent (Figs. 7 and 8), 1 bivalent and 1 univalent (Figs. 9 and 11), and 3 univalents (Fig. 10). About 70 % of the cells observed showed 1 bivalent and 1 univalent (Table 1). In cells without a bivalent two B chromosomes tended to be close to each other. The occurrence of trivalents despite their relatively small size indicates that the 3 B chromosomes are homologous or partially homologous and have a common or similar origin.

The A chromosomes formed predominantly 15 bivalents, however, some irregularities were noted; about 6 % of PMCs showed 14 bivalents + 2 univalents and 1 % showed 13 bivalents + 4 univalents (Table 1). The degree of pollen stainability of about 86 % possibly reflected the slight

TABLE 1. -- B and A chromosome configuration in PMCs of the Anthurium warocqueanum parent

Spadix sample	B chromosomes				A chromosomes				
	1 III	1II+1I	3I	Total	15II	14II+2I	13II+4I	12II+6I	Total
1	1	68	31	100	93	6	1	0	100
2	2	69	29	100	88	9	3	0	100
3	0	76	24	100	96	4	0	0	100
Mean	1.0	71.0	28.0		92.3	6.3	1.3	0	

TABLE 2. -- Stainability of pollen grains of the *Anthurium warocqueanum* parent

Spadix sample	Stained	Unstained	Total
1	440 (88 %)	60 (12 %)	500
2	442 (88.4 %)	58 (11.6 %)	500
3	410 (82 %)	90 (18 %)	500
Mean	430.7 (86.1 %)	69.3 (13.9 %)	

Plate II. Somatic chromosomes and karyotype of the parent *Anthurium warocqueanum*.

Figure:

2. Somatic chromosomes of the parent *Anthurium warocqueanum* (2n=30+3B) (1650X)
3. Karyotype of the parent *Anthurium warocqueanum* (2n=30+3B) (2200X).

②

③

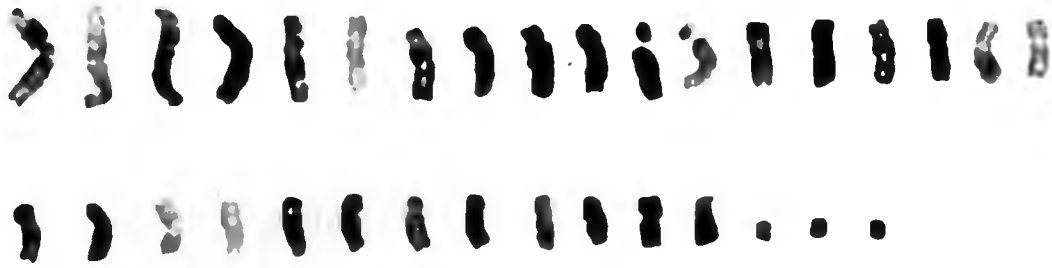

Plate III. Early meiosis (PMC) of the parent *Anthurium warocqueanum* (1650X).

Figure:

4. Interphase
5. Early prophase I
6. Diplotene (prophase I)
7. Diakinesis (prophase I), showing three B chromosomes as a trivalent.

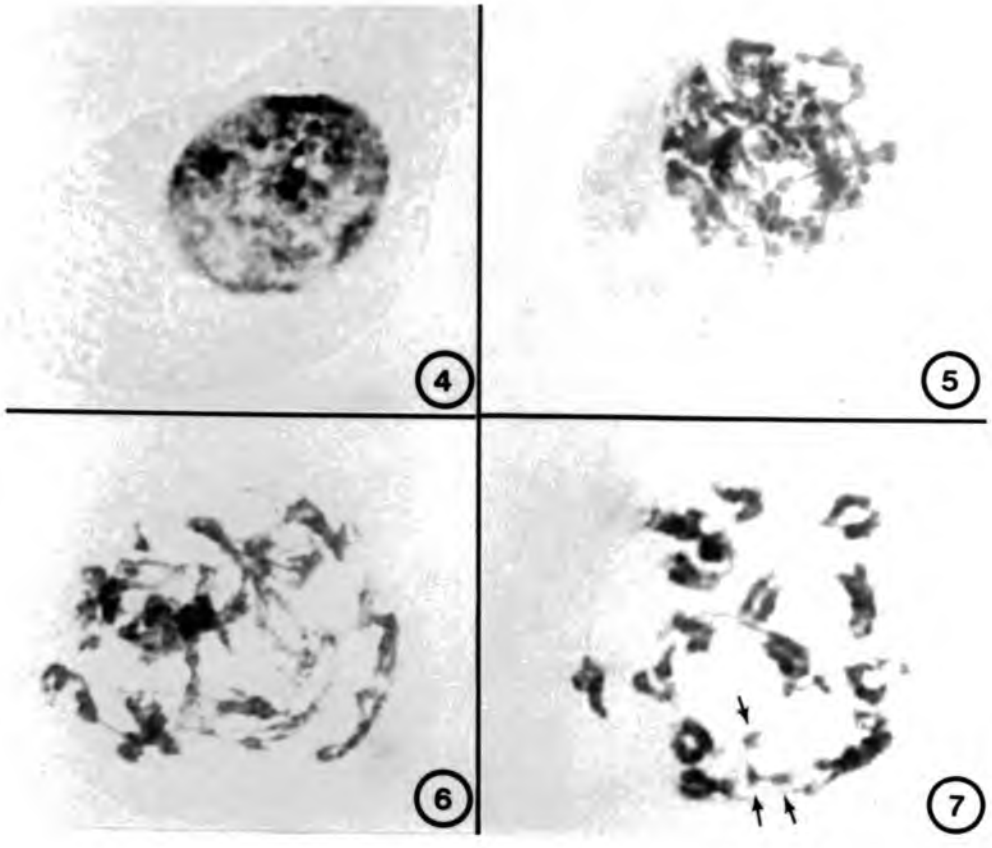
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Plate IV. Metaphase I (PMC) of the parent Anthurium warocqueanum (1650X).

Figure:

8. A chromosomes form 15 bivalents and B chromosomes form a trivalent (A-- 15 II and B-- 1 III) (polar view).
9. A chromosomes form 15 bivalents and B chromosomes form one bivalent and one univalent (A-- 15 II and B-- 1 II + 1 I) (polar view).
10. A chromosomes form 15 bivalents and B chromosomes form three univalents (A-- 15 II and B-- 3 I) (polar view).
11. B-- 1 II + 1 I (equatorial view).

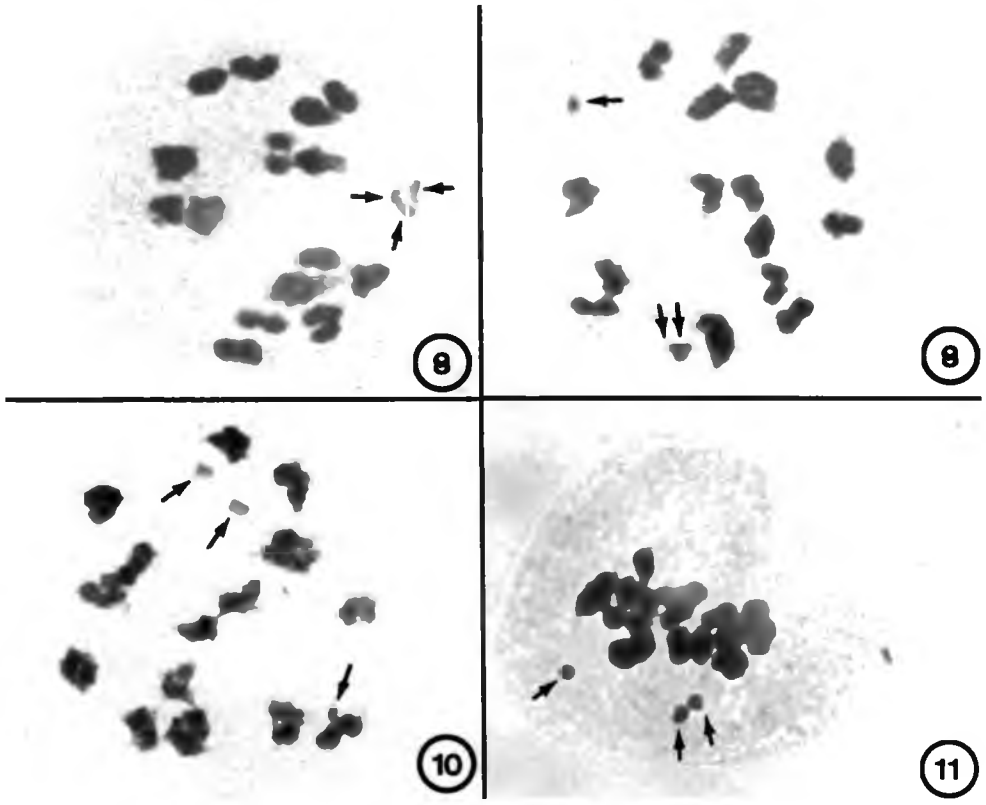
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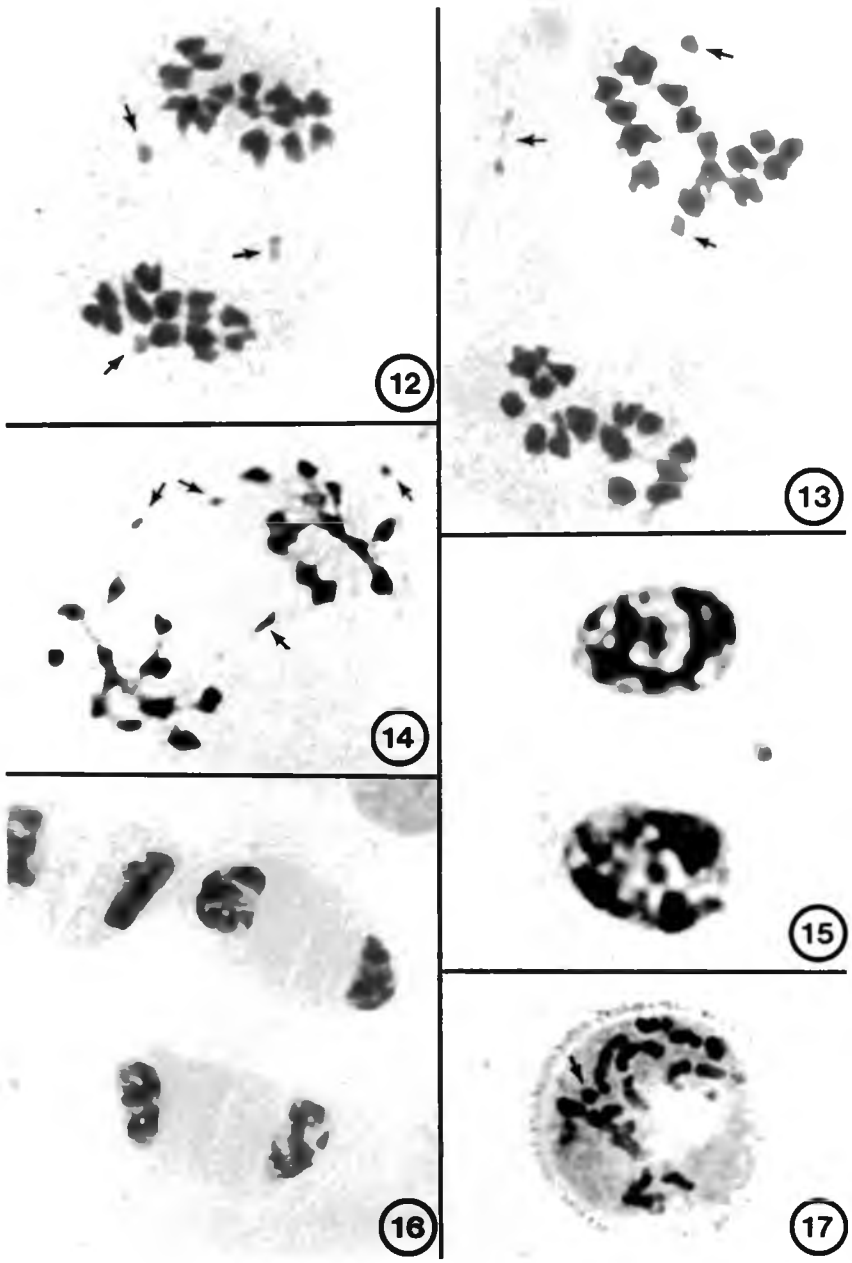
Plate V. Meiosis (PMC) of the parent Anthurium warocqueanum (1650X).

Figure:

12. Anaphase I, 2 Bs move toward opposite poles while univalent B chromosome lags at about metaphase plate.
13. Anaphase I, 2 Bs at the same pole and a lagging B showing its chromatids stating to divide from each other.
14. Anaphase I, showing separation of chromatids of B chromosome.
15. Telophase I, formation of micronucleus.
16. Tetrad formation at the end of meiosis.
17. Pollen mitosis, showing the presence of B chromosome.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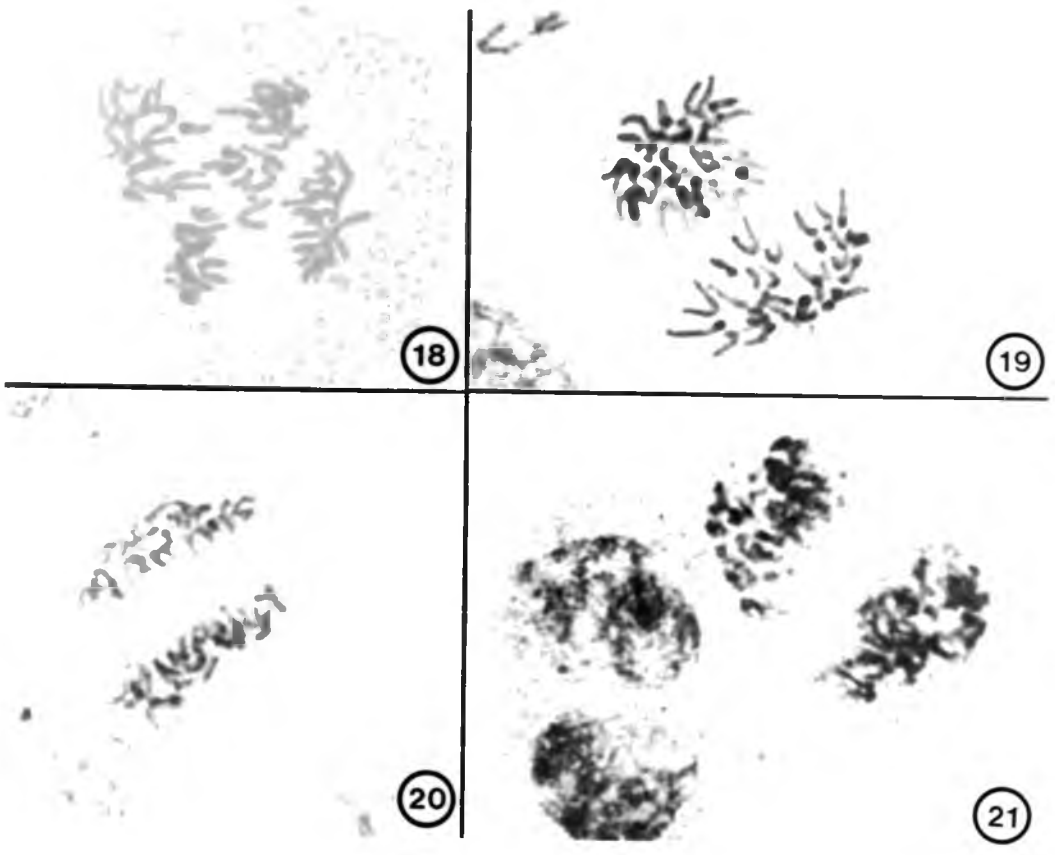
15
16
17

Plate VI. Somatic cell division of the parent *Anthurium warocqueanum* (1650X).

Figure:

18. Early anaphase.
19. Anaphase.
20. Late anaphase.
21. Telophase.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21

irregularity in meiosis of the A chromosomes (Table 2).

A clue to the transmission mechanism of B chromosomes can be observed in anaphase I of meiosis where univalent B chromosomes showed a tendency to lag (Fig. 12), or sometimes chromatids started to divide from each other (Figs. 13 and 14). The irregular distribution and lagging of B chromosomes at anaphase I may have led to the formation of micronuclei at telophase I (Fig. 15). An example of normal tetrad formation at the end of meiosis of the parent is shown in Figure 16. Observation of pollen mitosis showed the presence of B chromosomes in some pollen grains, confirming the transmission of Bs through the male parent (Fig. 17).

Unlike their irregular movements at meiosis, B chromosomes were found to be stable in somatic cell divisions (Figs. 18 - 21).

Distribution of B chromosomes in the offspring

Chromosome number determination from pollen mother cells of 94 selfed offspring of Anthurium warocqueanum with 2n=30+3B showed seven categories of B chromosome ranging from 0 to 6 B (Table 3). The distribution was calculated to be normal (Table 4), although 2B plants exhibited the highest frequency. The results indicate that B chromosomes were transmitted from both male and female gametes, which confirms the report by Kaneko and Kamemoto (1979). The higher number of 2B offspring over 3B

TABLE 3. -- Frequency of offspring with various numbers of B chromosomes determined from pollen mother cells

	Number of B chromosomes							
	0B	1B	2B	3B	4B	5B	6B	Total
Number of plants	1	7	36	26	18	5	1	94
Percent of plants	1.1	7.4	38.3	27.7	19.1	5.3	1.1	100

TABLE 4. -- Calculation of the Goodness of Fit X^2 for the distribution of selfed offspring of Anthurium warocqueanum for each B-chromosome class

Number of B chromosomes	Frequencies		$\frac{(f - \hat{f})^2}{\hat{f}}$
	Observed f	Expected $\hat{f}$	
0	1	2.7	1.070
1	7	11.2	1.575
2	36	24.6	5.283
3	26	29.0	0.310
4	18	18.5	0.014
5	5	6.3	0.078
6	1	1.2	0.033
Total	94	93.5	8.363

$X^2 = 8.363$, d.f. = 7 - 3 = 4. $p > 0.05$[z]

z The hypothesis of normality is not rejected at 5 % significance level.

offspring might be explained from observation of B chromosome behavior in meiosis of the parent. At metaphase I 2 B chromosomes tend to pair, distributing each B chromosome equally to opposite poles during anaphase I, while a lagging univalent seems to form a micronucleus or microcyte and ultimately be eliminated. As a result, a pollen grain would frequently contain only one B chromosome at the end of meiosis. Assuming that the same phenomenon occurs in female gametogenesis to often produce an embryo with one B chromosome, it can be predicted that 2B offspring will appear with highest frequency.

In some plants, especially those with a higher number of B chromosomes, there was found to be some discrepant counts of B chromosomes between somatic cells and pollen mother cells (Table 5). These differences are assumed to be errors in counts of B chromosomes from somatic cells due to the presence of loose satellites from satellite chromosomes. The satellites are about the same size as B chromosomes.

Figures 22 - 28 show somatic chromosomes of seven different types of offspring where 0B, 1B, 2B, 3B, 4B, 5B, and 6B are observed. In figures 29 - 35, the karyotypes of each category of offspring are shown.

Comparing somatic cells with pollen mother cells, the B chromosomes in Anthurium warocqueanum seem to be stable in number.

TABLE 5. -- Counts of B chromosomes in pollen mother cells (PMC) and somatic cells of offspring

Plant no.		PMC	Somatic cells	Plant no.		PMC	Somatic cells
1	(#57)	0	0	46	(# 4)	3	3
2	(# 6)	1	1	47	(#23)	3	3
3	(#55)	1	1	48	(#24)	3	3
4	(#68)	1	1	49	(#25)	3	3
5	(#88)	1	1	50	(#26)	3	3
6	(#27)	1	2	51	(#28)	3	3
7	(#32)	1	2	52	(#37)	3	3
8	(#43)	1	2	53	(#38)	3	3
9	(#13)	2	2	54	(#54)	3	3
10	(#15)	2	2	55	(#62)	3	3
11	(#19)	2	2	56	(#64)	3	3
12	(#29)	2	2	57	(#70)	3	3
13	(#33)	2	2	58	(#76)	3	3
14	(#41)	2	2	59	(#94)	3	3
15	(#46)	2	ca.2	60	(#102)	3	3
16	(#47)	2	2	61	(#104)	3	3
17	(#51)	2	2	62	(# 1)	3	4
18	(#63)	2	2	63	(# 3)	3	4
19	(#72)	2	2	64	(# 9)	3	4
20	(#80)	2	2	65	(#10)	3	4
21	(#92)	2	2	66	(#31)	3	4
22	(#96)	2	2	67	(#65)	3	4
23	(#97)	2	2	68	(#75)	3	4
24	(#99)	2	2	69	(#90)	3	4
25	(#101)	2	2	70	(#103)	3	4
26	(# 2)	2	3	71	(#52)	3	5
27	(# 5)	2	3	72	(#21)	-	3
28	(#12)	2	3	73	(#60)	-	3
29	(#18)	2	3	74	(#71)	-	3
30	(#20)	2	3	75	(#74)	-	3
31	(#30)	2	3	76	(#93)	-	3
32	(#39)	2	3	77	(#82)	4	2
33	(#45)	2	3	78	(#36)	4	3
34	(#48)	2	3	79	(#69)	4	3
35	(#67)	2	3	80	(#35)	4	4
36	(#73)	2	3	81	(#40)	4	4
37	(#86)	2	3	82	(#44)	4	4
38	(#89)	2	3	83	(#50)	4	4
39	(#49)	2	4	84	(#66)	4	4
40	(#56)	2	4	85	(#79)	4	4
41	(#58)	2	4	86	(#95)	4	4
42	(#81)	2	4	87	(#100)	4	4
43	(#87)	2	4	88	(# 7)	4	5
44	(#27)	2	-	89	(#11)	4	5
45	(#98)	-	2	90	(#14)	4	5

TABLE 5. -- (Continued) Counts of B chromosomes in pollen mother cells (PMC) and somatic cells of offspring

Plant no.	PMC	Somatic cells
91 (#17)	4	5
92 (#34)	4	5
93 (#78)	4	5
94 (#84)	4	5
95 (#22)	-	4
96 (#77)	-	4
97 (#91)	-	4
98 (#61)	5	3
99 (#42)	5	5
100 (#59)	5	5
101 (# 8)	5	ca.6
102 (#16)	5	ca.6
103 (#85)	-	5
104 (#83)	6	5

Plate VII. Somatic chromosomes of offspring (1650X).

Figure:

22. 0B offspring.

23. 1B offspring.

24. 2B offspring.

25. 3B offspring.

26. 4B offspring.

27. 5B offspring.

28. 6B offspring.

22
23
24
25
26
27
28

Plate VIII. Karyotypes of offspring (2200X).

Figure:

29. 0B offspring.

30. 1B offspring.

31. 2B offspring.

32. 3B offspring.


29
30
31
32

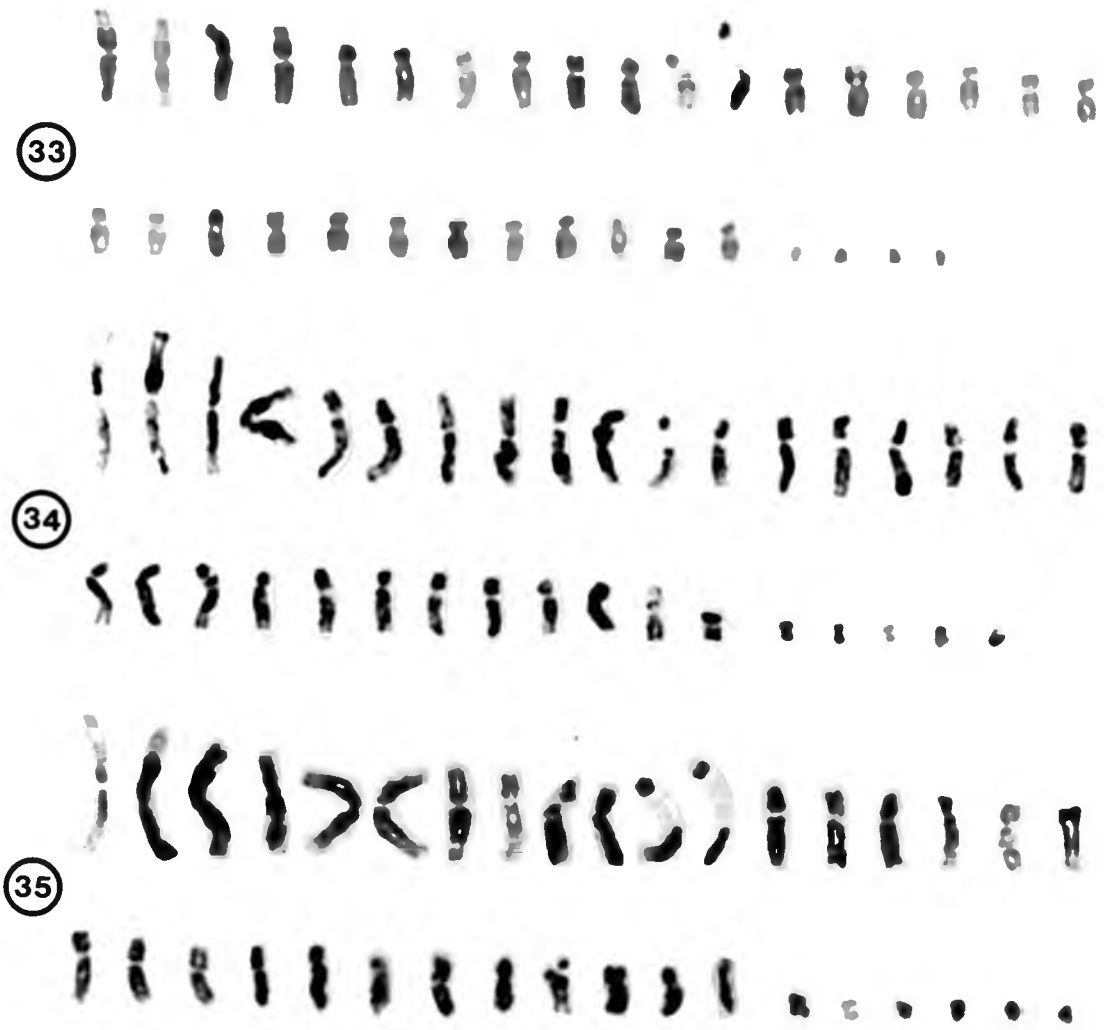
Plate IX. Karyotypes of offspring (2200X).

Figure:

33. 4B offspring.

34. 5B offspring.

35. 6B offspring.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Meiotic behavior of B chromosomes of offspring

Different behaviors of B chromosomes, as well as their effect on A chromosomes, were observed in PMCs of selfed offspring of Anthurium warocqueanum (Figs. 36 - 68). Figure 36 shows metaphase I of the plant lacking B chromosomes where 30 A chromosomes form 15 bivalents. The mean A chromosome configuration at diakinesis and metaphase I of the 0B plant was found to be 14.92II + 0.16I from examination of 25 pollen mother cells (Table 6a).

The single B chromosome present in the 1B offspring can be seen at diakinesis (Fig. 37) and at metaphase I (Fig. 38). The B chromosome tended to lag at anaphase I (Fig. 39). Studies on late anaphase I of the same 1B plant revealed variable behavior of the B chromosome. In Figure 40 the presence of the B chromosome is not discernible, indicating that it had moved toward one of the two poles and was included within a set of basic chromosomes. Frequently, the B chromosome lagged at or near the metaphase plate (Fig. 41); however, the separation of chromatids toward the two opposite poles was also observed (Fig. 42). Stickness of B chromosomes can be seen in Figure 43 where the association of the B chromosome with a part of the A chromosome at the center of the cell causes an uneven distribution of the A chromosomes, possibly leading to the formation of a micronucleus at the end of meiosis. Although it cannot be concluded that the production of sterile pollen is due to

TABLE 6a. -- Chromosome configurations at diakinesis and metaphase I of 0B and 1B offspring (25 PMCs per spadix were examined)

Offspring		Configuration of A chromosomes		
		Range	Mode (No. of cells)	Mean
0B		15II - 14II+2I	15II(23)	14.92II+0.16I
1B	#1	15II - 14II+2I	15II(23)	14.92II+0.16I
	#2	15II - 14II+2I	15II(24)	14.96II+0.08I
	#3	15II	15II(25)	15II
	#4	15II	15II(25)	15II
	#5	15II - 14II+2I	15II(24)	14.96II+0.08I
	#6	15II	15II(25)	15II
	#7	15II	15II(25)	15II
			mean	14.977II+0.046I

Plate X. Meiosis (PMC) in 0B and 1B offspring of *Anthurium warocqueanum* (1650X).

Figure:

36. Metaphase I of 0B offspring.
37. Diakinesis of 1B offspring.
38. Metaphase I of 1B offspring.
39. Anaphase I of 1B offspring, showing a B chromosome lagging.

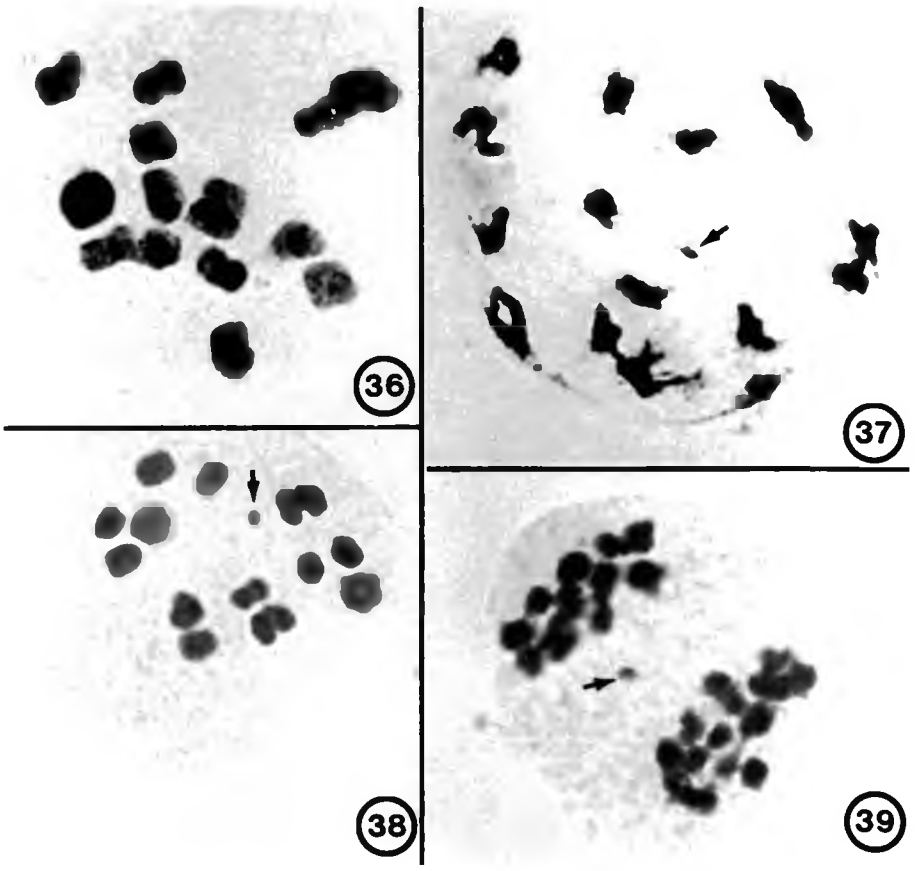
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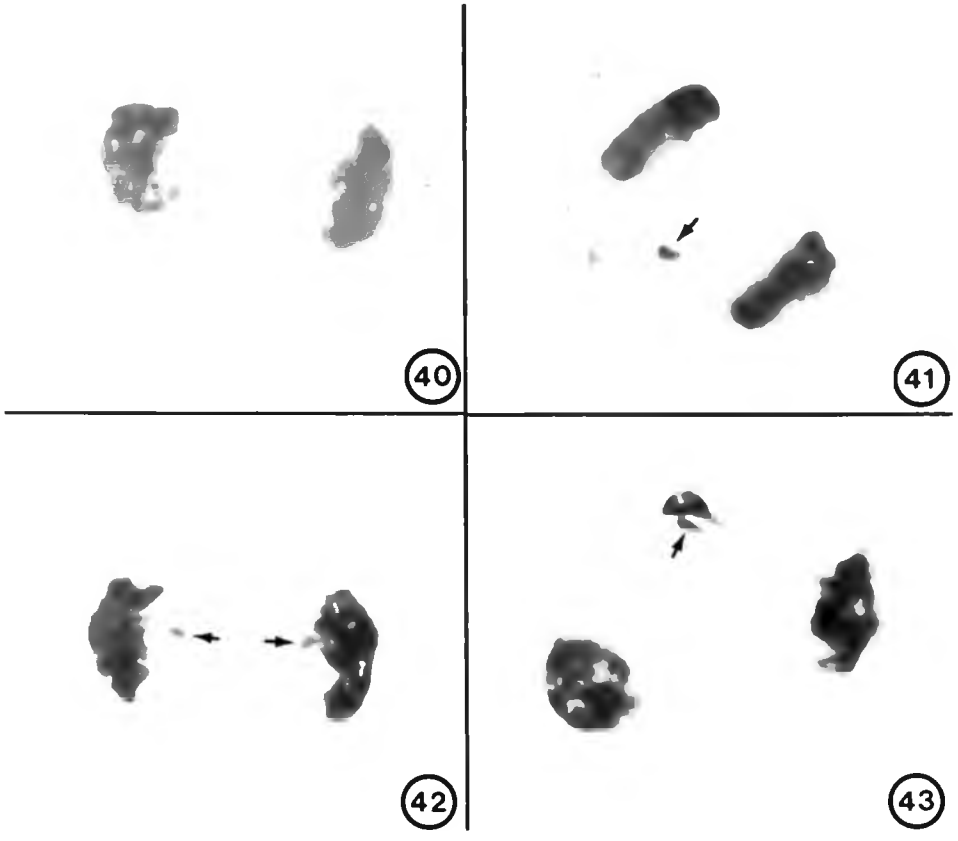
Plate XI. Late anaphase I in 1B offspring of *Anthurium warocqueanum* (1650X).

Figure:

40. No lagging B chromosomes.
41. Lagging B chromosome at the metaphase plate.
42. Separation of a B chromosome.
43. Association of A and B chromosomes.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41
42
43

the effect of a B chromosome on the A chromosomes, it is assumed that a B chromosome participates in inducing this phenomenon. The mean meiotic configuration of the 1B plant shows almost perfect pairing of the two sets of homologous A chromosomes (Table 6a).

The largest number of the offspring (38.3 %) had two B chromosomes (Table 3). A close association of the two B chromosomes was found in some cells at diakinesis (Fig. 44) and at metaphase I (Fig. 45). Within a single plant the 2Bs may or may not be paired (Figs. 46 and 47; Table 6b). The later stages of meiosis have again displayed some irregular types of behavior of B chromosomes, such as lagging at anaphase I (Fig. 48), formation of micronuclei after the reduction division (Fig. 49) and the production of unfunctional microspores at the end of meiosis (Fig. 50). The configurations of the A chromosomes in 2B offspring were similar to those of 0B and 1B plants (Table 6b).

The three B chromosomes of 3B offspring exhibited meiotic behavior similar to that of the parent (Figs. 51 - 55; Table 6c). At diakinesis and metaphase I they form three univalents (Fig. 51), one bivalent and one univalent (Fig. 52), or one trivalent, as observed in two cases (Table 6c). Figures 53 - 55 show irregular meiotic behavior of the 3B plant: lagging of one B chromosome (Figs. 53 and 54), and the formation of micronuclei (Fig. 55). The lagging B chromosome at anaphase I in

TABLE 6b. -- Chromosome configurations at diakinesis and metaphase I of meiosis of 2B offspring

Offspring	No. of cells according to configurations of 2 B chromosomes			Configuration of A chromosomes		
	1 II	2 I	Total	Range	Mode (No. of cells)	Mean
#1	6	19	25	15II - 14II+2I	15II(24)	14.96II+0.08I
#2	4	21	25	15II - 14II+2I	15II(19)	14.76II+0.48I
#3	5	20	25	15II - 14II+2I	15II(22)	14.88II+0.24I
#4	8	17	25	15II - 13II+4I	15II(23)	14.88II+0.24I
#5	8	17	25	15II - 14II+2I	15II(21)	14.84II+0.32I
#6	11	14	25	15II - 14II+2I	15II(22)	14.88II+0.24I
#7	4	21	25	15II - 14II+2I	15II(18)	14.72II+0.56I
#8	8	17	25	15II - 14II+2I	15II(23)	14.92II+0.16I
#9	9	16	25	15II - 14II+2I	15II(17)	14.68II+0.64I
#10	4	21	25	15II - 12II+6I	14II+2I(12)	14.16II+1.68I
#11	4	21	25	15II - 13II+4I	15II(15)	14.48II+1.04I
#12	11	14	25	15II - 13II+4I	15II(23)	14.88II+0.24I
#13	14	11	25	15II - 14II+2I	15II(22)	14.88II+0.24I
#14	5	20	25	15II - 14II+2I	15II(22)	14.88II+0.24I
#15	13	12	25	15II	15II(25)	15II
#16	10	15	25	15II - 12II+6I	15II(21)	14.76II+0.48I
#17	14	11	25	15II - 13II+4I	15II(21)	14.80II+0.40I
#18	11	14	25	15II - 14II+2I	15II(17)	14.68II+0.64I
#19	10	15	25	15II - 14II+2I	15II(24)	14.96II+0.08I
#20	9	16	25	15II - 14II+2I	15II(16)	14.64II+0.72I
#21	6	19	25	15II - 12II+6I	15II(11) 14II+2I(11)	14.24II+1.52I
#22	13	12	25	15II - 14II+2I	15II(21)	14.84II+0.32I

TABLE 6b. -- (Continued) Chromosome configurations at diakinesis and metaphase I of meiosis of 2B offspring

Offspring	No. of cells according to configurations of 2 B chromosomes			Configuration of A chromosomes		
	1 II	2 I	Total	Range	Mode (No. of cells)	Mean
#23	19	6	25	15II	15II(25)	15II
#24	15	10	25	15II - 14II+2I	15II(22)	14.88II+0.24I
#25	17	8	25	15II - 13II+4I	15II(19)	14.72II+0.56I
#26	13	12	25	15II - 14II+2I	15II(22)	14.88II+0.24I
#27	20	5	25	15II - 14II+2I	15II(22)	14.88II+0.24I
#28	21	4	25	15II - 14II+2I	15II(23)	14.92II+0.16I
#29	9	16	25	15II - 13II+4I	15II(19)	14.64II+0.72I
#30	14	11	25	15II	15II(25)	15II
#31	13	12	25	15II - 14II+2I	15II(24)	14.96II+0.08I
#32	18	7	25	15II - 14II+2I	15II(23)	14.92II+0.16I
#33	23	2	25	15II	15II(25)	15II
#34	18	7	25	15II - 14II+2I	15II(22)	14.88II+0.24I
#35	13	12	25	15II - 14II+2I	15II(24)	14.96II+0.08I
#36	18	7	25	15II	15II(25)	15II
						mean 14.816II+0.369I

TABLE 6c -- Chromosome configurations at diakinesis and metaphase I of meiosis of 3B offspring

Offspring	No. of cells according to configurations of 3 B chromosomes				Configuration of A chromosomes		
	1 III	1 II + 1 I	3 I	Total	Range	Mode (No. of cells)	Mean
#1	-	12	13	25	15II - 13II+4I	15II(22)	14.84II+0.32I
#2	-	14	11	25	15II - 12II+6I	15II(9)	13.92II+2.16I
#3	-	15	10	25	15II - 14II+2I	15II(21)	14.84II+0.32I
#4	-	22	3	25	15II - 13II+4I	15II(21)	14.80II+0.40I
#5	-	12	13	25	15II - 13II+4I	15II(22)	14.84II+0.32I
#6	-	16	9	25	15II - 14II+2I	15II(21)	14.84II+0.32I
#7	-	19	6	25	15II - 14II+2I	15II(24)	14.96II+0.08I
#8	-	21	4	25	15II	15II(25)	15II
#9	-	10	15	25	15II - 12II+6I	15II(12)	14.20II+1.60I
#10	-	20	5	25	15II - 14II+2I	15II(23)	14.92II+0.16I
#11	-	22	3	25	15II - 14II+2I	15II(22)	14.88II+0.24I
#12	-	14	11	25	15II - 14II+2I	15II(23)	14.92II+0.16I
#13	0	16	9	25	15II - 11II+8I	15II(22)	14.76II+0.48I
#14	0	16	9	25	15II - 14II+2I	15II(23)	14.92II+0.16I
#15	0	18	7	25	15II - 13II+4I	15II(23)	14.88II+0.24I
#16	0	17	8	25	15II - 14II+2I	15II(24)	14.96II+0.08I
#17	0	25	0	25	15II - 14II+2I	15II(24)	14.96II+0.08I
#18	1	21	3	25	15II - 14II+2I	15II(22)	14.88II+0.24I
#19	0	13	12	25	15II	15II(25)	15II
#20	0	17	8	25	15II	15II(25)	15II
#21	0	23	2	25	15II	15II(25)	15II
#22	0	18	7	25	15II - 14II+2I	15II(24)	14.96II+0.08I

TABLE 6c -- (Continued) Chromosome configurations at diakinesis and metaphase I of meiosis of 3B offspring

Offspring	No. of cells according to configurations of 3 B chromosomes				Configuration of A chromosomes		
	1 III	1 II + 1 I	3 I	Total	Range	Mode (No. of cells)	Mean
#23	1	19	5	25	15II	15II(25)	15II
#24	0	16	9	25	15II	15II(25)	15II
#25	0	16	9	25	15II - 14II+2I	15II(24)	14.96II+0.08I
							mean 14.850II+0.30II

Plate XII. Meiosis (PMC) in 2B offspring of *Anthurium warocqueanum* (1650X).

Figure:

44. Diakinesis
45. Metaphase I, 2 Bs paired (polar view).
46. Metaphase I, 2 Bs paired (equatorial view).
47. Metaphase I, 2 Bs unpaired (equatorial view).

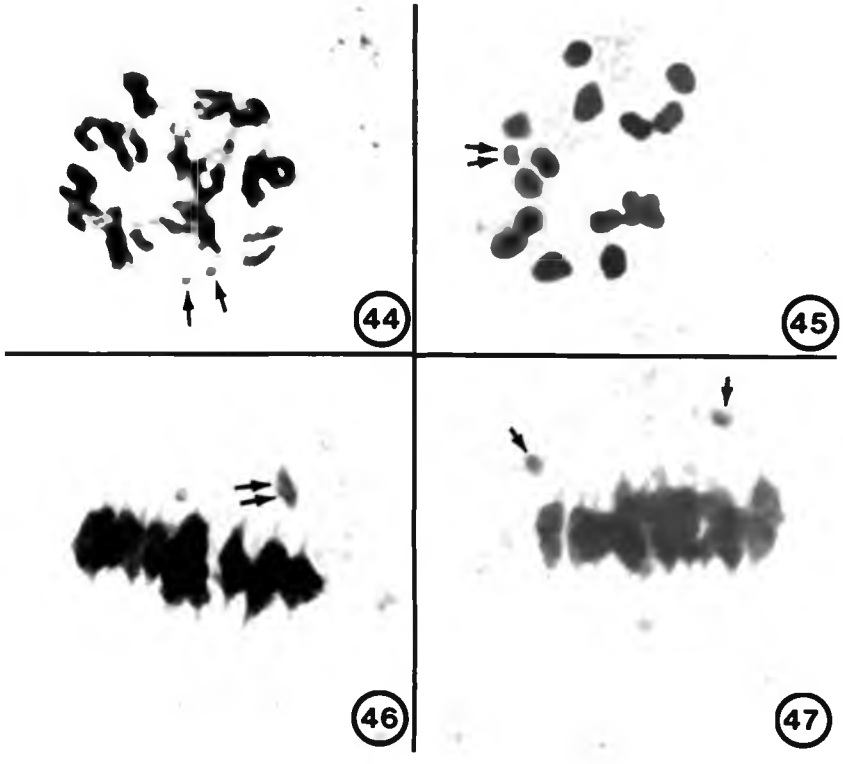
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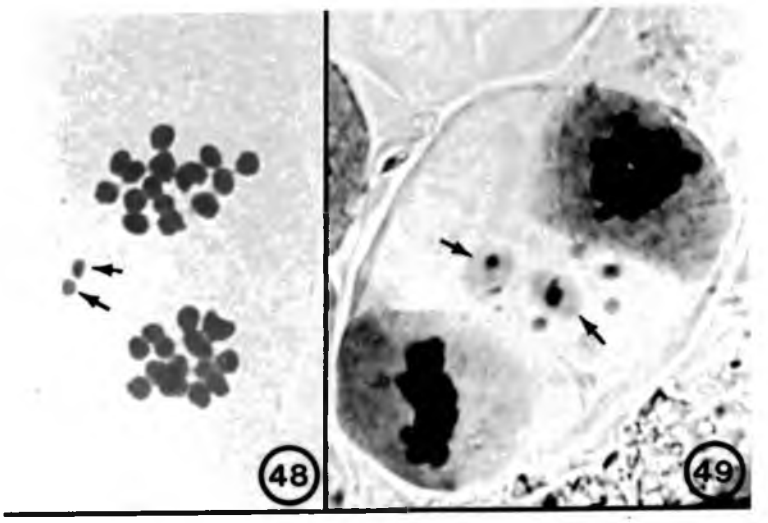
Plate XIII. Meiosis (PMC) in 2B offspring of *Anthurium warocqueanum* (1650X).

Figure:

48. Anaphase I, 2 Bs are lagging.
49. Metaphase II, formation of two micronuclei.
50. The end of meiosis, tetrad plus extra small microspore.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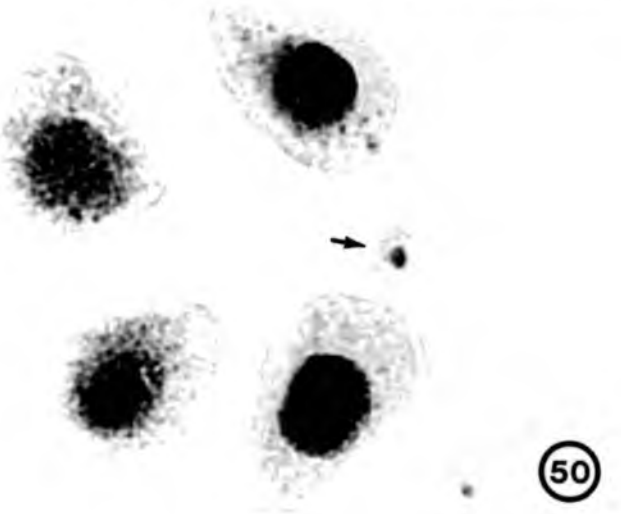
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Plate XIV. Meiosis (PMC) in 3B offspring of *Anthurium warocqueanum* (1650X).

Figure:

51. Diakinesis, A--15 bivalents (15 II) and B--3 univalents (3 I).
52. Metaphase I, A--15 bivalents (15 II) and B--1 bivalent and 1 univalent (1 II + 1 I).
53. Anaphase I, an univalent B is lagging.
54. Anaphase I, association of A and B chromosomes.
55. Late anaphase II, formation of micronuclei.

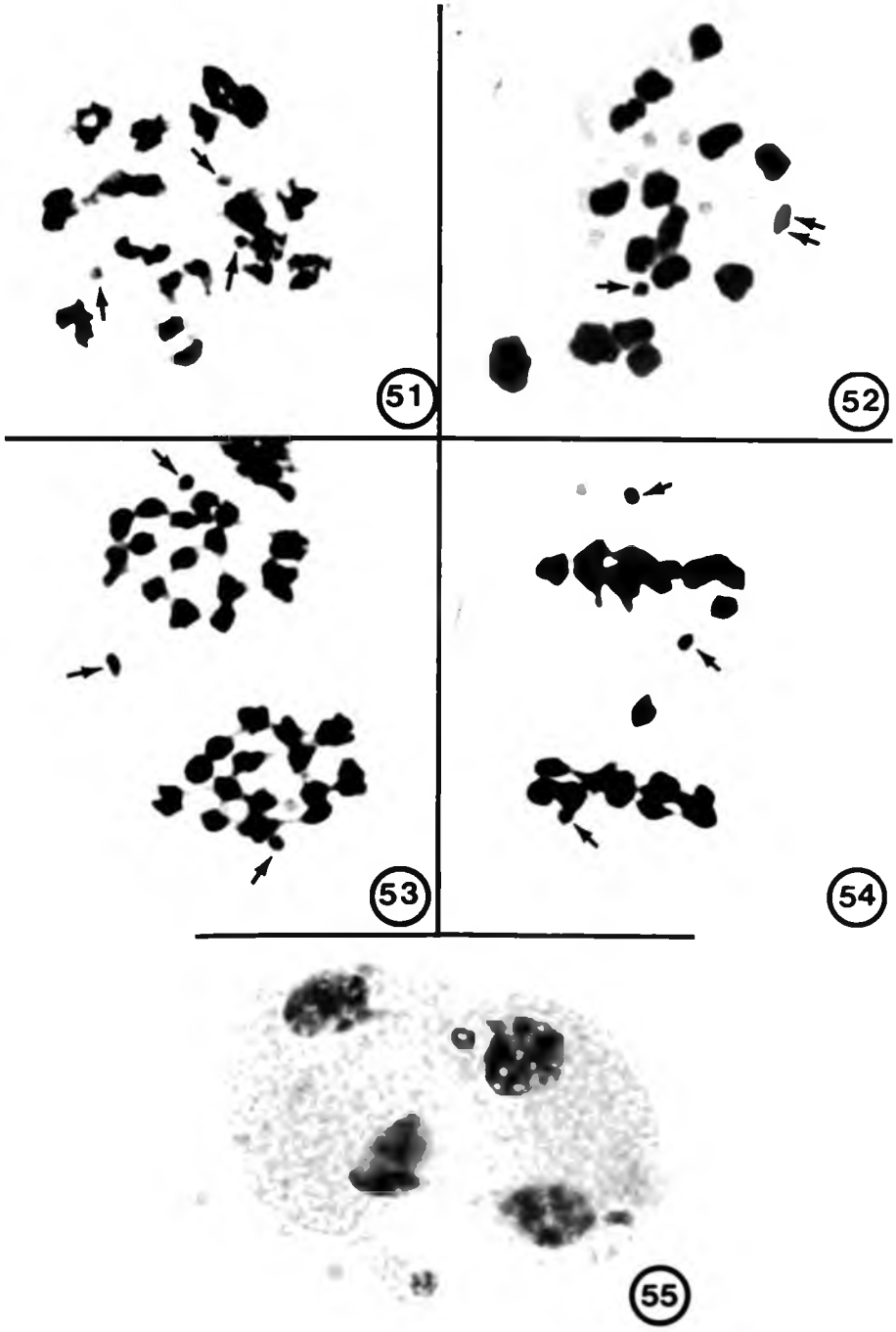
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Figure 54 seems to be affecting the movement of A chromosomes by its physical affinity with the As through a slender threadlike formation, thus delaying the distribution of A chromosomes to the opposite poles.

At diakinesis and metaphase I of the 4B offspring, four classes of B-chromosomal configuration were found (Table 6d): one trivalent and one univalent (Fig. 56), two bivalents (Fig. 57), one bivalent and two univalents (Figs. 58 and 59), and four univalents. Association of higher numbers of B chromosomes by themselves such as formation of trivalents or quadrivalents, were hardly seen, whereas 2 B pairings were predominant. In Figures 58 and 59, a pair of A chromosomes appear as two univalents, possibly indicating that a higher number of B chromosomes can prevent homologous pairings of A chromosomes in the meiotic process.

The meiotic configurations of 5 and 6 B chromosomes were also examined and tabulated in Table 6d. In 5B plants, the formations of two bivalents and one univalent (Fig. 61), one bivalent and three univalents (Fig. 62) and five univalents (Fig. 63) were commonly observed while one trivalent and one bivalent was found in only one case. The 6B plant exhibited four types of B-chromosomal configuration: three bivalents (Fig. 65), two bivalents and two univalents, one bivalent and four univalents, and six univalents (Figs. 66 and 67). Later meiotic stages of higher-numbered B plants again showed variable behavior of

TABLE 6d. -- Chromosome configurations at diakinesis and metaphase I of meiosis of 4B, 5B, and 6B offspring

Offspring	No. of cells according to configurations of B chromosomes					Configuration of A chromosomes		
						Range	Mode (No. of cells)	Mean
4B	1 III + 1 I	2 II	1 II + 2 I	4 I	Total			
#1	-	2	10	13	25	15II - 12II+6I	15II(11)	14.12II+1.76I
#2	-	1	7	4	12	15II - 13II+4I	15II(7)	14.50II+1.00I
#3	-	2	15	8	25	15II - 12II+6I	15II(17)	14.40II+1.20I
#4	-	1	10	14	25	15II - 12II+6I	15II(10)	13.96II+2.08I
#5	-	4	19	2	25	15II - 12II+6I	15II(21)	14.72II+0.56I
#6	-	4	16	5	25	15II - 13II+4I	15II(17)	14.60II+0.80I
#7	-	7	10	8	25	15II - 13II+4I	15II(22)	14.84II+0.32I
#8	-	6	18	1	25	15II - 13II+4I	15II(17)	14.64II+0.72I
#9	1	4	9	11	25	15II - 14II+2I	15II(24)	14.96II+0.08I
#10	1	13	8	3	25	15II - 13II+4I	15II(22)	14.84II+0.32I
#11	0	17	7	1	25	15II - 13II+4I	15II(24)	14.92II+0.16I
#12	0	4	12	9	25	15II - 14II+2I	15II(23)	14.92II+0.16I
#13	0	12	10	3	25	15II - 14II+2I	15II(24)	14.96II+0.08I
#14	0	6	15	4	25	15II - 14II+2I	15II(24)	14.96II+0.08I
#15	0	7	14	4	25	15II - 14II+2I	15II(23)	14.92II+0.16I
								mean 14.684II+0.632I

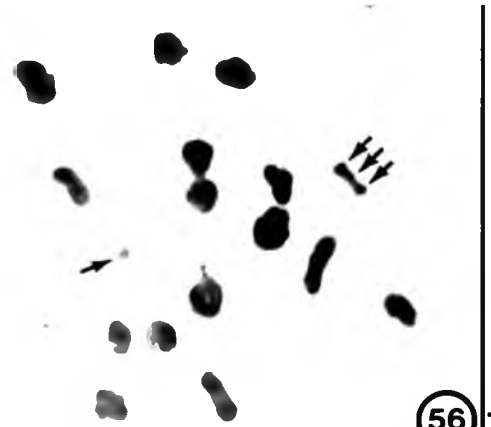
TABLE 6d. -- (Continued) Chromosome configurations at diakinesis and metaphase I of meiosis of 4B, 5B, and 6B offspring

Offspring	No. of cells according to configurations of B chromosomes					Configuration of A chromosomes		
						Range	Mode (No. of cells)	Mean
5B	1 III + 1 II	2 II + 1 I	1 II + 3 I	5 I	Total			
#1	-	4	17	4	25	15II - 11II+8I	14II+2I(10)	12.56II+2.48I
#2	-	7	12	6	25	15II - 12II+6I	14II+2I(14)	13.88II+2.24I
#3	-	5	9	11	25	15II - 9II+12I	13II+4I(7)	12.20II+5.60I
#4	1	14	9	1	25	15II - 14II+2I	15II (21)	14.84II+0.32I
								mean 13.370II+2.660I
6B	3 II	2 II + 2 I	1 II + 4 I	6 I	Total			
	3	11	7	4	25	15II - 10II+10I	13II+4I(9)	13.32II+3.36I

Plate XV. Meiosis (PMC) in 4B offspring of *Anthurium warocqueanum* (1650X).

Figure:

56. Metaphase I, A-- 15 bivalents (15 II) and B-- 1 trivalent and 1 univalent (1 III + 1 I).
57. Metaphase I, A-- 15 bivalents (15 II) and B-- 2 bivalents (2 II).
58. Metaphase I, A-- 14 bivalents and 2 univalents (14 II + 2 I) and B-- 1 bivalent and 2 univalents (1 II + 2 I).
59. Metaphase I, A-- 14 bivalents and 2 univalents (14 II + 2 I) and B-- 1 bivalent and 2 univalents (1 II + 2 I) (equatorial view).
60. Anaphase I, showing irregular movements of B chromosomes.



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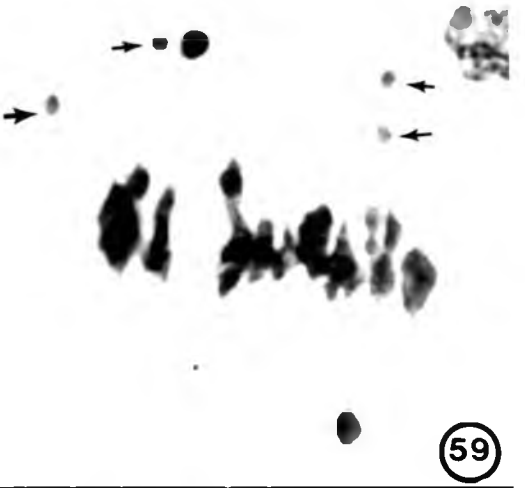
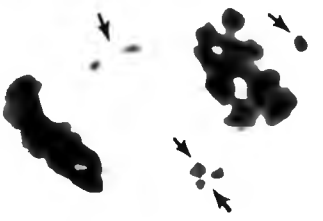


59



60

Plate XVI. Meiosis (PMC) in 5B offspring of *Anthurium warocqueanum* (1650X).

Figure:

61. Metaphase I, A-- 15 bivalents (15 II) and B-- 2 bivalents and 1 univalent (2 II + 1 I).
62. Metaphase I, A-- 15 bivalents (15 II) and B-- 1 bivalent and 3 univalents (1 II + 3 I).
63. Metaphase I, A-- 15 bivalents (15 II) and B-- 5 univalents (5 I).
64. Anaphase I.

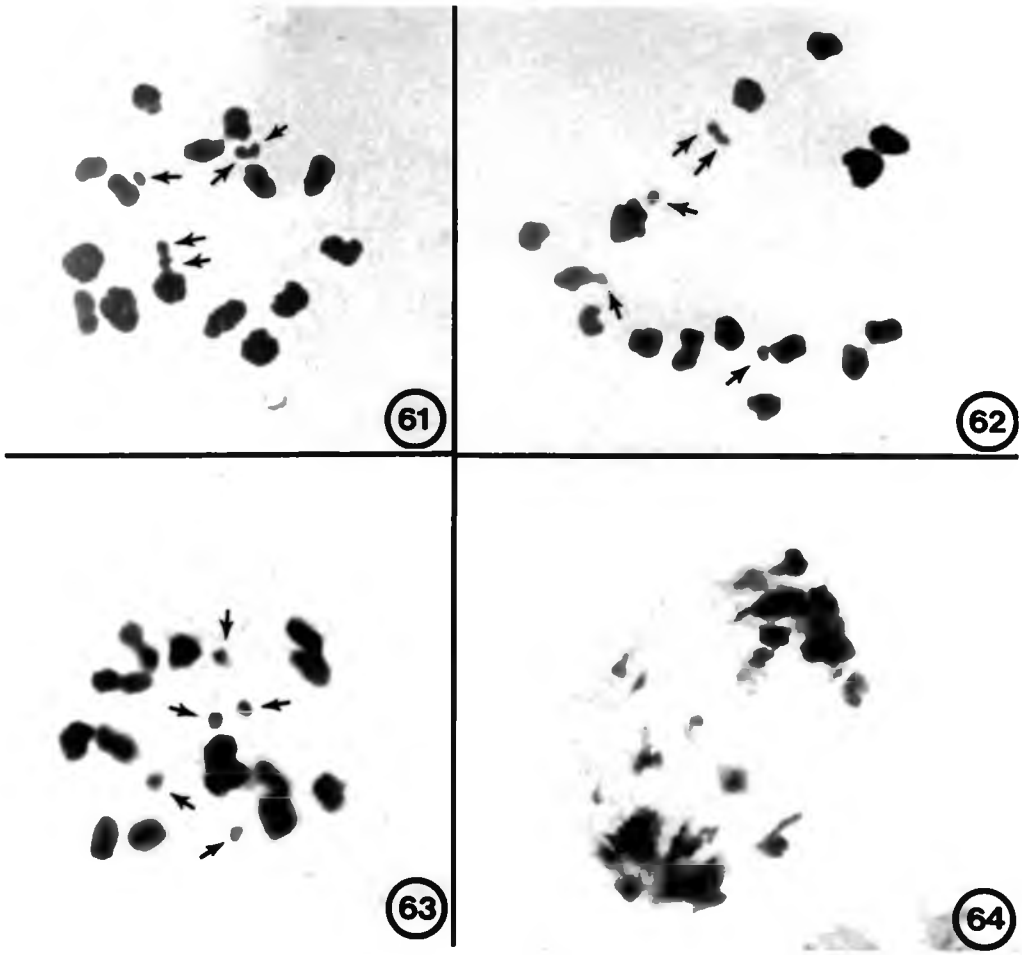
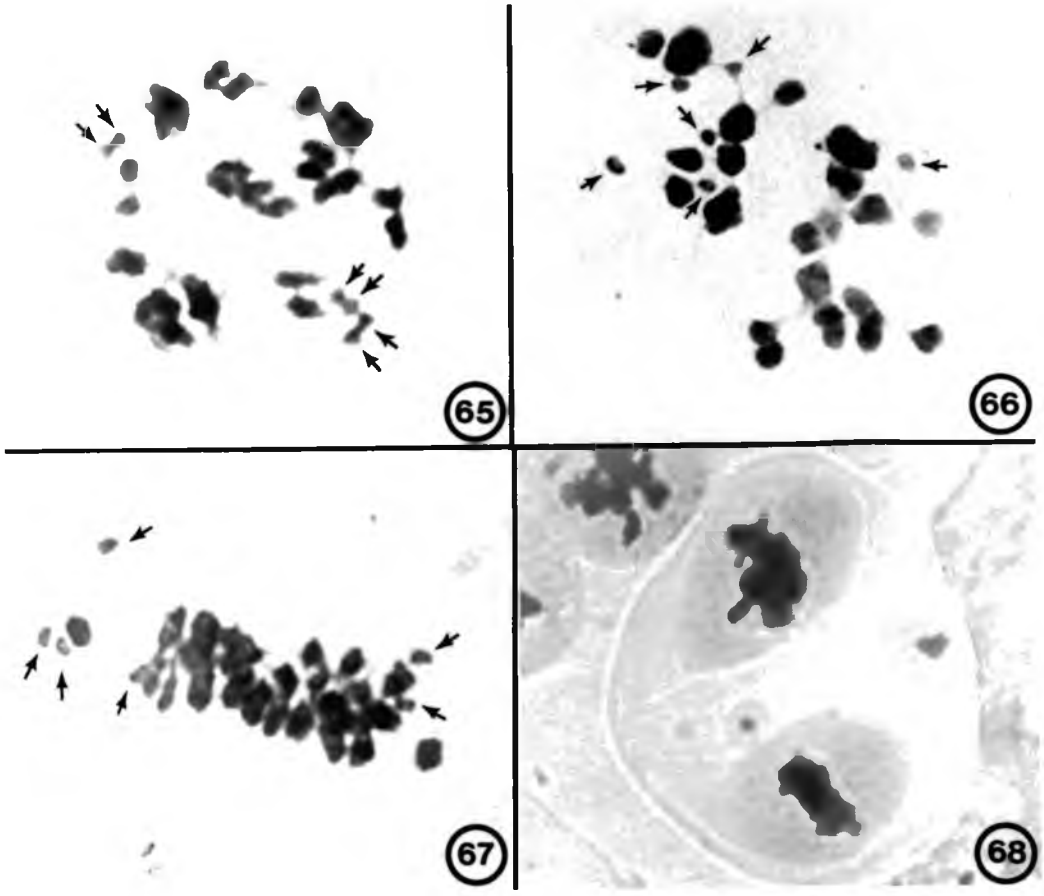

61
62
63
64

Plate XVII. Meiosis (PMC) in 6B offspring of *Anthurium warocqueanum* (1650X).

Figure:

65. Metaphase I, A-- 15 bivalents (15 II) and B-- 3 bivalents (3 II).
66. Metaphase I, A--12 bivalents and 6 univalents (6 I) and B-- 6 univalents (6 I) (polar view).
67. Metaphase I, B-- 6 univalents (6 I) (equatorial view).
68. Metaphase II, formation of micronuclei.


65
66
67
68

Bs, which could lead to the formation of micronuclei and microcytes. For example, anaphase I of 4B and 5B offspring are shown in Figures 60 and 64, respectively, exhibiting B-laggards in both cases. The unequal size of two micronuclei are observable in the 6B plant at metaphase II (Fig. 68). Table 6(a-d) shows that PMCs of 5 and 6B offspring exhibit a wider range of A-chromosomal configuration and a lower degree of bivalent formations.

Observations of pollen mother cells in the offspring have revealed several interesting features of B chromosomes in Anthurium warocqueanum. When two or more B chromosomes are present, 2 Bs are frequently associated together during the early meiotic stages, forming bivalents or positioning themselves close to each other. B bivalents generally undergo normal disjunction at anaphase I; however, in some cases, the paired Bs lag at or near the metaphase plate or both move toward the same pole. Behavior of unpaired Bs at anaphase I is more unpredictable than that of paired ones. They may move toward either pole, lag, or two sister chromatids may separate to opposite poles. Lagging B chromosomes possibly result in the formation of micronuclei at the end of reduction division.

An interaction between A and B chromosomes was found to exist to some extent. Although no pairing between the two classes of chromosomes was observed during meiotic activities earlier than metaphase I, some physical

TABLE 7. -- Comparison of A chromosome configurations at meiosis of offspring

Offspring	Overall mean configuration of A chromosomes
0B(1)*	14.92II+0.16I
1B(7)	14.977II+0.046I
2B(36)	14.816II+0.369I
3B(25)	14.850II+0.301I
4B(15)	14.684II+0.632I
5B(4)	13.370II+2.660I
6B(1)	13.32II+3.36I

* Number of offspring observed are shown in parenthesis.

affinities were seen in anaphase I where Bs were delaying the movements of A chromosomes. With the higher number of Bs, normal A-bivalent formations seemed to be reduced (Table 7), enhancing production of abnormal pollen grains.

Phenotypic effects of B chromosomes

Means of observations and standard errors for four characters (leaf length, leaf width, increase in stem length, and first flowering date) were calculated in each B-class and tabulated in Table 8. The similar mean values for each class indicate that there are no odd and even effects of B chromosomes in Anthurium warocqueanum, as reported for straw weight and tiller number of rye (Muntzing, 1963). Regression analysis showed that the number of Bs had not affected any plant characteristic (Table 9).

Plant species possessing B chromosomes, in general, show no effects of the B chromosomes on their phenotypes (Jones, 1975). In this experiment it is concluded that B chromosomes in Anthurium warocqueanum had no distinguishable influence on leaf length, leaf width, increase in stem length, or the first flowering date.

TABLE 8. -- Phenotypic effects of B chromosomes in *Anthurium warocqueanum*

Character	Date of measurement Time interval or Days to first flower		Number of B chromosomes						
			0(1)*	1(7)	2(36)	3(26)	4(18)	5(5)	6(1)
Leaf length	Date of measurement								
	Aug. 4, 1978	$\bar{x}$	34.00	28.04	29.24	30.42	27.48	29.74	28.20
		$S_{\bar{x}}$		1.596	0.757	0.793	1.099	2.249	
	Feb. 6, 1979	$\bar{x}$	37.60	34.17	36.37	36.92	35.33	37.92	37.50
		$S_{\bar{x}}$		1.076	0.834	0.801	0.853	2.499	
	Aug. 9, 1979	$\bar{x}$	36.70	39.51	38.56	39.65	38.72	40.54	37.20
		$S_{\bar{x}}$		1.714	0.797	0.705	0.892	2.056	
Leaf width	Aug. 4, 1978	$\bar{x}$	11.40	8.49	9.04	9.33	8.41	8.60	8.00
		$S_{\bar{x}}$		0.537	0.244	0.280	0.331	0.636	
	Feb. 6, 1979	$\bar{x}$	12.30	10.86	11,46	11.70	10.91	11.54	10.50
		$S_{\bar{x}}$		0.530	0.277	0.298	0.312	0.788	
	Aug. 9, 1979	$\bar{x}$	12.80	13.40	13.28	13.36	13.39	12.90	11.70
		$S_{\bar{x}}$		0.587	0.289	0.313	0.453	0.995	

* Number of offspring observed are shown in parenthesis.

TABLE 8. -- (Continued) Phenotypic effects of B chromosomes in Anthurium warocqueanum

Character	Date of measurement, Time interval or Days to first flower		Number of B chromosomes						
			0(1)*	1(7)	2(36)	3(26)	4(18)	5(5)	6(1)
Increase in stem length	Time interval								
	Aug. 15, 1978 - Feb. 6, 1979	$\bar{x}$	9.30	10.27	8.84	8.70	7.06	8.48	12.00
		$S_{\bar{x}}$		1.038	0.409	0.485	0.823	1.206	
	Feb. 6, 1979 - Aug. 9, 1979	$\bar{x}$	4.70	9.33	7.21	7.28	7.89	10.24	9.40
		$S_{\bar{x}}$		1.220	0.694	0.626	0.579	2.022	
	Aug. 15, 1978 - Aug. 9 1979	$\bar{x}$	14.00	19.60	16.04	15.98	14.95	18.72	21.40
		$S_{\bar{x}}$		2.122	0.859	1.024	1.148	2.795	
Days to flower	Days from germination to first flower	$\bar{x}$	897.0	990.4	978.6	1003.8	1002.2	952.0	1069.0
		$S_{\bar{x}}$		21.60	12.92	23.24	21.05	21.68	

* Number of offspring observed are shown in parenthesis.

TABLE 9. -- Regression analysis of the relationship between B chromosomes and plant characters of *Anthurium warocqueanum*

Character	Date of measurement, Time interval or Days to first flower	Statistical values				
		r	b	Sb	t	p
Leaf length	Date of measurement					
	Aug. 4, 1978	0.081	0.373	0.478	0.780	0.437ns
	Feb. 6, 1979	0.173	0.847	0.500	1.694	0.094ns
	Aug. 9, 1979	0.140	0.699	0.515	1.357	0.178ns
Leaf width	Date of measurement					
	Aug. 4, 1978	-0.008	-0.012	0.155	-0.080	0.936ns
	Feb. 6, 1979	0.084	0.138	0.171	0.806	0.422ns
	Aug. 9, 1979	0.093	0.173	0.193	0.895	0.373ns
Increase in stem length	Time interval					
	Aug. 15, 1978 - Feb. 6, 1979	-0.127	-0.323	0.264	-1.223	0.224ns
	Feb. 6, 1979 - Aug. 9, 1979	0.143	0.460	0.332	1.382	0.170ns
	Aug. 15, 1978 - Aug. 9, 1979	0.004	0.017	0.498	0.033	0.974ns
Days to flower	Days from germination to first flower	0.200	22.61	11.55	1.958	0.053ns

ns indicates that values are not significant at the p=0.05 level.

LITERATURE CITED

Ayonoadu, U. and H. Rees. 1968. The influence of B-chromosomes on chiasma frequencies in Black Mexican sweet corn. Genetica 39:75-81.

Battaglia, E. 1964. Cytogenetics of B chromosomes. Caryologia 17:245-299.

Bosemark, N.O. 1954. On accessory chromosomes in Festuca pratensis. I. Cytological investigations. Hereditas 40:346-376.

_____ 1956. On accessory chromosomes in Festuca pratensis. III. Frequency and geographical distribution of plants with accessory chromosomes. Hereditas 42:189-210.

_____ 1957. Further studies on accessory chromosomes in grasses. Hereditas 43:236-297.

_____ 1967. Edaphic factors and the geographical distribution of accessory chromosomes in Phleum phleoides. Hereditas 57:239-262.

Cameron, F.M. and H. Rees. 1967. The influence of B chromosomes on meiosis in Lolium. Heredity 22:446-450.

Chang, C.C. and G.Y. Kikudome. 1974. The interaction of knobs and B chromosomes of maize in determining the level of recombination. Genetics 77:45-54.

Carlson, W.R. 1978. The B chromosomes of corn. Ann. Rev. Genet. 16:5-23.

Chilton, M.D. and B.J. McCarthy. 1973. DNA from maize with and without B chromosomes: a comparative study. Genetics 74:605-614.

Darlington, C.D. 1956. Natural population and breakdown of classical genetics. Proc. Roy. Soc. Ser. B. 146: 350-364.

Darlington, C.D. and A.P. Wylie. 1955. Chromosome atlas of flowering plants. Allen and Unwin Ltd. London.

Dnyansagar, V.R. and A.R. Pingle. 1979. Effects of fragments and probable origin of B chromosomes in Solanum viarum Dunal. Cytologia 44:561-569.

Engler, A. 1905. Araceae-Pothoideae. Das Pflanzenr. IV. 21:53-330.

Evans, G.M. and A.J. Macefield. 1973. The effect of B-chromosomes on homoeologous pairing in species hybrids. I. Lolium temulentum X Lolium perenne. Chromosoma (Berl.) 41:63-73.

Federov, A.A. ed. 1969. "Chromosome numbers of flowering plants." Acad. Sci. USSR Leningrad.

Fisk, E.L. 1925. The chromosomes of Zea mays. Proc. Nat. Acad. Sci. U.S. 11:352-356.

Fröst, S. 1958a. The geographical distribution of accessory chromosomes in Centaurea scabiosa. Hereditas 44:75-111.

_____ 1958b. Studies of the genetical effects of accessory chromosomes in Centaurea scabiosa. Hereditas 44:112-122.

_____ 1959. The cytological behavior and mode of transmission of accessory chromosomes in Plantago serraria. Hereditas 45:191-210.

_____ 1962. Numerical increase of accessory chromosomes in Crepis conyzaefolia. Hereditas 48: 667-676.

_____ 1969. The inheritance of accessory chromosomes in plants, especially in Ranunculus acris and Phleum nodosum. Hereditas 61:317-326.

Gaiser, L.O. 1927. Chromosome numbers and species characters in Anthurium. Proc. and Tran. Roy. Soc. Canada 21:1-137.

Gill, J.J.B., B.M.G. Jones, C.J. Marchant, J. Mcleish, and D.J. Ockendon. 1972. The distribution of chromosome races of Ranunculus ficaria L. in the British isles. Ann. Bot. (London) 36:31-47.

Grun, P. 1959. Variability of accessory chromosomes in native populations of Allium cernuum. Amer. J. Bot. 46:218-224.

Håkansson, A. 1948. Behavior of accessory rye chromosomes in the embryo sac. Hereditas 34:35-59.

Hanson, G.P. 1969. B chromosome stimulated crossing over in maize. Genetics 63:601-609.

Hasegawa, N. 1934. A cytological study on 8-chromosome rye. Cytologia 6:68-77.

Hovin, A. W. and H.D. Hill. 1966. B-chromosomes, their origin and relation to meiosis in interspecific Lolium hybrids. Amer. J. Bot. 53:702-708.

Jackson, R.C. and Newmark, P. 1960. Effects of supernumerary chromosomes on production of pigment in Haplopappus gracilis. Science 132:1316-1317.

Joshi, S. and S.S. Raghuvanshi. 1970. Accessory chromosomes in a tree Ficus krishnae. Ann. Bot. (London) 34:1037-1039.

Jones, R.N. 1975. B-chromosome systems in flowering plants and animal species. Int. Rev. Cytol. 40: 1-100.

_____ 1976. Genome organization in higher plants. In Chromosome Today. Proc. 5th. Oxford Chromosome Conf. 117-130.

Kaneko, K.and H. Kamemoto. 1978. Cytological studies of 'Kaumana' and 'Uniwai' Anthurium. J. Amer. Soc. Hort. Sci. 103(5):699-701.

_____and _____ 1979. Karyotype and B chromosomes of Anthurium warocqueanum. J. Hered. 70:271-272.

Kootin-Sanwu, M. and S.R.J. Woodell. 1969. Supernumerary chromosomes in Caltha palustris. In Chromosome Today. Proc. 2nd. Oxford Chromosome Conf. 196-196.

Kuwada, Y. 1915. Ueber die chromosomenzahl von Zea mays. Bot. Mag. (Tokyo) 29:83-89.

Longley, A.E. 1927. Supernumerary chromosomes in Zea mays. J. Agri. Res. 35:769-784.

_____ 1938. Chromosomes of maize from North American Indians. J. Agri. Res. 56:177-195.

Mehra, P.N. and K.S. Bawa. 1968. B-chromosome in some Himalayan hard woods. Chromosoma (Berl.) 25:90-95.

Mooring, J.S. 1960. A cytogenetic study of Clarkia unguculata. II. Supernumerary chromosomes. Amer. J. Bot. 47:847-854.

Moss, J.P. 1969. B-chromosomes and breeding systems. In Chromosome Today. Proc. 2nd. Oxford Chromosome Conf. p. 268.

Müntzing, A. 1950. Accessory chromosome in rye populations from Turkey and Afghanistan. Hereditas 36:507-509.

_____ 1957. Frequency of accessory chromosomes in rye strains from Iran and Korea. Hereditas 43:682-685.

_____ 1963. Effects of accessory chromosomes in diploid and tetraploid rye. Hereditas 49:371-426.

_____ 1974. Accessory chromosomes. Ann. Rev. Genet. 8:243-266.

Paliwal, R.L. and Hyde, B.B. 1959. The association of a single B chromosome with male sterility in Plantago coronopus. Amer. J. Bot. 46:460-466.

Parker, J.S. 1976. The B-chromosome system of Hypochoeris maculata. I. B-distribution, meiotic behavior and inheritance. Chromosoma (Berl.) 59:167-177.

Pfitzer, P. 1957. Chromosomenzahlen von Araceen. Chromosoma 8:436-446.

Randolph, L.F. 1941. Genetic characteristics of the B chromosomes in maize. Genetics 26:608-631.

Rapp, K. 1979. Supernumerary chromosomes in Alopecurus pratensis L. I. A cytological and cytogenetic study in populations and diallel crosses. Hereditas 91:31-48.

Rees, H. and R.N. Jones. 1977. Chromosome Genetics. Univ. Park Press.

Reeves, R.G. 1925. Chromosome stidies of Zea mays L. Proc. Iowa Acad. Sci. 32:171-175.

Rimpan, J. and R.B. Flavell. 1976. The repeated sequence DNA of B chromosomes of rye. In Chromosome Today. Proc. 5th. Oxford Chromosome Conf. 147-157.

Röthlisberger, E. 1970. Verteilung der B-chromosomen und Blutentwicklung bei Crepis capillaris. Ber. Schweiz. Bot. Ges. 80:195-224.

Rutishauser, A. and E. Röthlisberger. 1966. Boosting mechanism of B-chromosomes in Crepis capillaris. In Chromosome Today. Proc. 1st. Oxford Chromosome Conf. 28-30.

Sharma, A. and U.C. Bhattacharyya. 1961. Structure and behavior of chromosomes in species of Anthurium with special reference to the accessory chromosomes. Proc. Natl. Inst. Sci. India, Pt. B, Biol. Sci. 27:317-328.

Sheffer, R.D. and H. Kamemoto. 1976a. Chromosome numbers in the genus Anthurium. Amer. J. Bot. 63:74-81.

_____ and _____ 1976b. Cross compatibility in the genus Anthurium. J. Amer. Soc. Hort. Sci. 101(6):709-713.

Swanson, C.P. 1943. Secondary association of fragment chromosomes in generative nucleus of Tradescantia and its bearing on their origin. Bot. Gaz. (Chicago) 105:108-112.

Tanaka, R. and T. Matsuda. 1972. A high occurrence of accessory chromosomal type in Tania laxiflora, Ochidaceae. Bot. Mag. Tokyo 85:43-49.

Teoh, S.B., H. Rees and J. Hutchison. 1976. B chromosome selection in Lolium. Heredity 37(2):207-213.

Tsuchiya, T. and M. Tanaka. 1962. Chromosome studies in five species of Araceae. Chr. Inf. Ser. 3:36-38.

Ward, E.J. 1973. The heterochromatic B chromosome of maize: the segments affecting recombination. Chromosoma 43:177-186.

Wedberg, H.L., H. Lewis and C.S. Venkatesh. 1968. Translocation heterozygotes and supernumerary chromosomes in wild populations of Clarkia williamsonii. Evolution 22:93-107.

Zohary, D. and I. Ashkenazi. 1958. Different frequencies of supernumerary chromosomes in diploid populations of Dactylis glomerata in Israel. Nature (London) 182:477-478.